Aquifoliaceae

Aquifoliaceae Bercht. & J. Presl, Přir. Rostlin 2: 440 (1825), nom cons.

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Trees or shrubs, rarely climbers; base of trunk straight, rarely with small buttresses; stem without latex or resin. Leaves usually evergreen, rarely deciduous, spirally arranged, rarely opposite or subopposite, simple, coriaceous to chartaceous, stipulate; plants dioecious. Flowers small, hypogynous, regular, unisexual by abortion, without disk, often 4–6-merous or up to 23-merous, in axillary cymose inflorescences, sometimes reduced to one flower. Sepals small, more or less connate at the base or rarely distinct; petals imbricate, mostly connate at the base, rarely free; stamens usually isomerous, alternating with the petals, and connate at the base. Carpels isomerous, united to form a superior ovary, with as many locules as carpels, each generally containing one ovule. Fruit a drupe, red, black, yellow, white, orange or purple, rarely green but mostly variously red, containing 1–6(−23) pyrenes. Seed small with abundant oily and proteinaceous endosperm, without starch.

A family of irregular cosmopolitan distribution; comprising one genus with more than 600 species.

Vegetative Morphology and Anatomy. The stem is straight and up to 30 m high, and rarely has small buttresses. The leaves are simple, evergreen or rarely deciduous, spirally arranged (2/5 for the leaves, bracts and cymes), rarely opposite or subopposite, orbiculate, oblanceolate, elliptic, ovate or lanceolate. Their length is approximately 2–15 cm, with a maximum of 35 cm in *I. megaphylla* from Sarawak and a minimum of 4 mm in *I. microphylla*. The base of the lamina is acute to obtuse, the apex truncate to acute, often acuminate, and the margin can be serrate, crenate, or entire, rarely spinose. Entire or spiny leaves can be present in the same species (e.g. *I. dipyrena* and *I. dimorphophylla*), or on the same plant (e.g. *I. aquifolium*). Stipules present, often caducous, small. Colleters (stipular on the node at the base of the leaves, standard and lachrymiform found on the leaf teeth or crenations, and sessile found on the margins of the floral bracts) have been identified in all the nine south American species studied (Gonzalez and Tarragó 2009). Stipular colleters replace stipules in these species. The leaves are coriaceous, rarely chartaceous, rarely pubescent, and punctate or not. Hairs simple and unicellular. The cortex is grey or ochre; when slashing the trunk, a thin green layer appears under the bark; the wood is yellow and its sap oxidizes rapidly, becoming black. This provides important field characters. Wood anatomy has been extensively studied by Baas (1973[1974]). Based on the observation of 81 species of *Ilex*, he concluded that the wood is characterized by conspicuous growth rings, and numerous narrow but relatively short vessel elements with few bars per perforation plate. Thickenings on vessel and fibre walls are spiral, and the fibre-tracheids frequently have numerous conspicuously bordered tangential wall pits (Baas 1973[1974]). *Ilex* has been cited as an example of a genus with trilacunar and unilacunar nodes (Baas 1975; Gonzalez and Tarragó 2009).

Inflorescence Structure. The flowering unit is the cyme, which can be reduced to one flower, or increased to up to 15–31 flowers. They are then solitary dichasia, thyrses or thyrsoids. Most of the species have thyrses, which are borne axillary, rarely terminally. Thyrses can be either non-proliferating, or proliferating when the post-flowering growth is vegetative. In case of the former, the axis of the thyrse can be contracted, so that it appears like a fascicle. Solitary dichasia are

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formed when the bracts of proliferating thyrses develop as leaves. Some species have simple thyrsoids whereas others have a "fascicle of thyrsoids" with alternate or decussate arrangements (Loizeau and Spichiger 1992).

The different classifications of *Ilex* have been based on the structure of the inflorescences. Loesener (1901, 1908) describes his subgenera and lower rank taxa on the basis of inflorescence type (e.g. solitary cymes, fascicles, racemes, or panicles). Hu (1949–1950) in her work on *Ilex* of China uses the cyme as the flowering unit, while Loizeau and Spichiger (1992) propose a phylogenetic classification.

Flower Morphology (Fig. 3). The flowers are hypogynous, regular, unisexual by abortion, often 4–6- or up to 23-merous in all whorls. The first flower of a cyme or the terminal flower of the thyrsoid can sometimes have one extra sepal and petal. The calyx is glabrous or pubescent, valvate, with small lobes and a more or less connate base. The calyx is persistent, rarely caducous (*I. mucronata*), semipersistent in *I. collina*. The corolla is often white or cream, rarely green, yellow, pink, purple, red or chocolate-coloured, with imbricate petals, and 1–10 mm in length. The petals are mostly connate at the base to up to half of their length. Some species have distinct petals (*I. collina*, *I. mucronata* and *I. vismiifolia*). In staminate flowers, the stamens alternate with the petals, are usually glabrous, and have a white filament. The anthers are basifixed and introrse. The sterile ovary is conical. In pistillate flowers, staminodes with sterile anthers are present; these are glabrous, rarely pubescent. The syncarpous ovary is globose, with as many locules as carpels. The style is terminal, very short or absent, and has a distinct stigma, with lobes poorly developed. One ovule is found in each locule, but additional aborted ovules can occur. The ovules are generally apical-axile, pendant, anatropous, apotropous, unitegmic, tenuinucellar, and with a large funiculus (Corner 1976). Because of the presence of staminodes in the pistillate flower and a sterile ovary in the staminate flower, some authors have considered *Ilex* to have bisexual flowers.

Embryology. Ives (1923) observed that the embryo is in a very immature condition when the drupe falls off the plant. It continues growing, very slowly, for a period of 8–12 months.

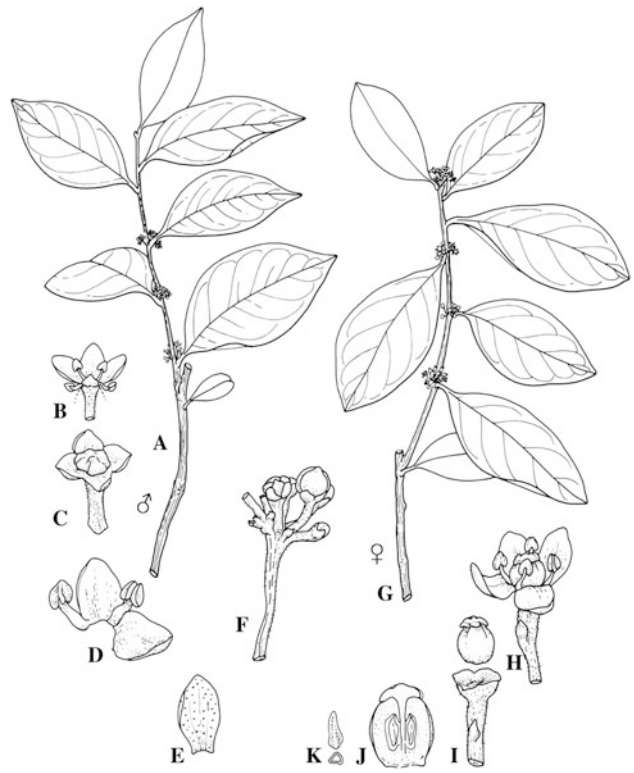

Fig. 3. Aquifoliaceae. **A–K** *Ilex vismiifolia*. **A** Branch with male inflorescences. **B** Male flower (one petal removed). **C** Male flower showing the calyx and the sterile ovary. **D** Male flower showing petals and stamens. **E** Petal. **F** Male inflorescence. **G** Branch with female inflorescences. **H** Female flower. **I** Female flower showing the ovary and the calyx. **J** Ovary, vertical section. **K** Pyrene. (Loizeau 1994, with permission from Boissiera)

Pollen. Pollen morphology has been extensively studied by Lobreau (1969). Pollen is tricolporate, isopolar, clavate, the exo-apertures are furrows with granular membranes, and the endo-apertures are oval and small. Individual pollen grains are between 17–47 µm × 18–48 µm, being larger in species of higher latitude or altitude (Lobreau-Callen 1977).

Pollination. Pollination usually is accomplished by insects (ants, bees, flies, wasps, butterflies and beetles) attracted by nectar produced at the base of the petals (Tsang and Corlett 2005).

Fruit and Seed Dispersal. Drupe with (1–)4–6 (−23) pyrenes, red, brown or black, usually globose; exocarp membranous or papery; mesocarp fleshy. Pyrenes with endocarp smooth, leathery, woody, or stony, striate, striate-sulcate, or rugose, and/or pitted (Chen and al. 2008). The fruits are

generally dispersed by birds. Germination in nature is delayed and requires from one to three years, with a germination of more or less half of the seeds (Ives 1923; Arrieta and Suárez 2004).

Karyology. Chromosome numbers of about 30 species of *Ilex*, mostly Asian, are known (Goldblatt 1981, 1984). Four different base numbers, $x = 17$, 18, 19, 20, were found. The majority of the species (21) have been reported to be diploid and to have $2n = 40$ chromosomes. Polyploidy occurs in some species: *I. pedunculosa* ($2n = 120$) is hexaploid, and *I. anomala* ($2n = 80$) and *I. verticillata* ($2n = 72$) are tetraploid. Most *Ilex* species have $2n = 40$ chromosomes.

Phytochemistry. Aquifoliaceae are sometimes saponiferous or tanniniferous, accumulate proanthocyanins and rarely cyanogenic compounds, but lack ellagic acid or iridoid compounds. Alikaridis (1987) studied the natural constituents of approximately 50 species worldwide; their stimulating and vomitive effects are related to the presence of very high quantities of purine bases (caffeine, theobromine, theophylline or adenine). Moreover, they contain vitamins (C, B1, B2), nicotinic acid, and carotene (Alikaridis 1987). According to Lewis et al. (1991), *I. guayusa* has the highest concentration of caffeine and methylxanthine known.

Affinities. Various hypotheses on the affinities of Aquifoliaceae have been published. Cronquist (1981, 1988) included Aquifoliaceae in Celastrales, near Celastraceae, and included *Phelline* (now Phellinaceae, Asterales) and *Sphenostemon* (now Paracryphiaceae, Paracryphiales) in the family. The inclusion in Celastrales was based on the morphology of the ovule with a dorsal raphe (Bentham and Hooker 1862) and the thick funiculus of Aquifoliaceae which was considered by Loesener (1908) to be homologous to the aril in the Celastraceae. Hallier (1903) placed Aquifoliaceae in his "Umbellifloren" (Umbelliferae/Apiaceae and their relatives) because of the small embryo and their common unisexuality. Baillon (1891) placed Aquifoliaceae between Ericaceae (because of the descendent placenta) and Ebenaceae (because of the drupaceous fruit). Tieghem (1898) placed Aquifoliaceae near Solanaceae because of the unitegmic ovule and the isomerous stamens alternating with the petals. Based on pollen, Lobreau (1969) regarded Aquifoliaceae as related to Gentianales and Campanulales. Finally, Dahlgren (1983) placed the family in Cornales because of the unitegmic ovules, whereas Thorne (1992) placed Aquifoliaceae in Theales, as did Baas (1973[1974], 1975) on the basis of wood anatomy. Based on several molecular phylogenetic studies, Aquifoliaceae are now well placed within the order Aquifoliales together with *Helwingia* and *Phyllonoma*, two genera with epiphyllous inflorescences, at the base of the euasterids (Savolainen et al. 2000a, 2000b; Soltis et al. 2000; Bremer et al. 2001). This placement of *Ilex* in a clade containing mostly gamopetalous plants is supported by the petals which are often connate at the base of the tube, and by the unitegmic ovules. Putative synapomorphies for the family may include the unisexual flowers and fleshy fruits (Bremer et al. 2001). Since *Nemopanthus* has been shown to be included in *Ilex* (Powell et al. 2000), Aquifoliaceae, Helwingiaceae and Phyllonomaceae are three monotypic families which may be better united in a single family (Powell et al. 2000; Savolainen et al. 2000a, 2000b; Soltis et al. 2000; Bremer et al. 2001). APG II (2003) and APG III (2009) proposed to keep Helwingiaceae and Aquifoliaceae as separate families.

Ecology and Distribution. *Ilex* occurs in all tropical areas of the world and extends into temperate regions to up to 63° N (America, Eurasia) and 35° S (America, Africa) (Baas 1974) from lowland to montane forests and up to 4000 m altitude in the Andes (Loizeau 1994). However, its distribution is very irregular and most species occur in South America and Asia. In China 204 species have been recorded (Chen et al. 2008). Andrews (2002) assumed that there are some 120 species in Southeast Asia, and Loizeau (1994) estimated that up to 300 species are found in America. There exist only two to three species in Europe, *I. aquifolium* (also in N Africa), *I. colchica* and *I. perado* subsp. *iberica*, one in Australia, *I. arnhemensis*, and one in Africa south of the Sahara, *I. mitis*. Twenty-six species are native to eastern North America (Kartesz 1994).

Palaeobotany. Pollen of a type attributed to *Ilex* is known from Turonian deposits in Australia

and Coniacian deposits in Africa. The pollen became cosmopolitan in the Palaeocene (Muller 1970) and pollen fossils have been found in Alaska, Iceland, western North America, southern South America, Siberia, New Zealand and southern Australia (Loizeau et al. 2005).

Economic Importance and Uses. Many species of *Ilex* are of horticultural importance and are widely grown in parks and gardens throughout the world for their foliage and decorative berries. These include (Andrews 1982, 1983a, 1983b, 1984a, 1984b, 1985, 1989, 1991, 1992) *I. aquifolium*, the common holly and its many cultivars, *I.* x *altaclerensis* (*I. aquifolium* x *I. perado*), *I. opaca*, the American holly (Eisenbeiss and Dudley 1973), *I. cornuta*, the horned holly, and *I. crenata*, the Japanese holly (Dudley and Eisenbeiss 1992). In China *I. purpurea* (*I. chinensis* is a misapplied name) is commonly planted as an ornamental tree, and the fruiting branches are used to decorate temple courts and halls from December to February. Large quantities of glossy-berried branches are sold at the Chinese New Year (Hu 1949–1950). The leaves of over 60 species of *Ilex* are used for beverages. The most widely known is a tea ("tereré") made from *I. paraguariensis*, the "Yerba Maté" or Paraguay Tea (Loizeau 1988). This species is native to Argentina, Uruguay, Paraguay and Brazil and is drunk throughout South America. The Yaupon or *I. vomitoria* from south-eastern North America and Mexico has been used by certain native North Americans who brewed a tea called the Black Drink or "Cassena". This was said to restore lost appetite, guarantee health and give courage and agility in war (Hudson 1979; Alikaridis 1987). Several species are known for their medicinal properties and the leaves of *I. aquifolium* were used as an infusion for smallpox, catarrh and pleurisy. The drupes acted as an emetic and purgative and have been used for dropsy and to prevent bleeding (Coles 1657). *Ilex guayusa* (see Phytochemistry) has been used for centuries as a medicine, an emetic and as a stimulant (Lewis et al. 1991). The roots of the widespread South-east Asian *I. cymosa* are said to have medicinal properties, especially in the treatment of fevers (Andrews 2002). *Ilex mitis*, the only species to occur naturally south of the Sahara, has been used as an enema for colic in children, as a purgative and is used in witchcraft (Andrews 1994). The wood of *I. aquifolium* is hard and white and has been much prized for ornamental use. The strong, straight shoots when stripped of their bark are made into whip handles and walking sticks (Dallimore 1908). The leaves were used as winter food crop for livestock in England, Wales and northwest France from the Middle Ages onwards (Spray 1981). The wood of *I. cissoidea* from Sumatra, Sulawesi and Borneo has been used as firewood and possibly for making matches. The dried leaves were pounded into a powder and used as a soap (Andrews, ined.), as were the leaves of *I. mitis*, while the wood is used for furniture, ceilings, brake blocks, railway sleepers or for firewood (Andrews 1994).

One genus:

Ilex L. Fig. 3

Ilex L., Sp. Pl.: 125 (1753); Loesener, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 78 (1901) and 89 (1908); Loizeau, Boissiera 48 (1994), rev. of Peruvian spp; Chen et al., Fl. China 11: 359–438 (2008), rev. of Chinese spp.; Manen et al., Pl. Syst. Evol. 235: 79–98 (2002), evol.; Manen et al., Mol. Phyl. Evol. 57: 961–977 (2010), evol. *Nemopanthus* Raf. (1819), nom. cons.

Molecular studies have shown hybridization and introgression even between distantly related lineages of the genus (Manen et al. 2002, 2010).

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